PLIOCENE GIRAFFOIDEA (MAMMALIA, ARTIODACTYLA) FROM THE CAPE PROVINCE

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(With 9 figures and 10 tables)

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CONTENTS

	PAGE
Introduction	325
Systematics	326
Sivatherium hendeyi sp. nov. . .	328
Giraffa cf. *G. jumae*	347
Discussion	352
Acknowledgements	352
References	353
Abbreviations	353

ABSTRACT

One sivathere species and one giraffine species, both represented by ossicones, teeth and postcranial elements, have been recovered from 'E' Quarry at Langebaanweg. The sivathere remains appear more primitive than those of the common African sivathere, *S. maurusium*, and warrant the creation of a new species. The giraffine species is less abundantly represented and is very similar to *Giraffa jumae* from east African Pliocene and Pleistocene localities. Other faunal evidence from 'E' Quarry suggests an early Pliocene age for the Varswater Formation. The *Sivatherium* species supports such an interpretation, suggesting that the Langebaanweg giraffoids are the earliest representatives yet reported of their respective genera.

INTRODUCTION

In recent years a number of Pliocene mammalian assemblages have been recorded from east and north Africa, but from South Africa only the local faunas from 'E' Quarry, Langebaanweg, are of undoubted Pliocene age. The younger material from Baard's Quarry at Langebaanweg is not considered in this paper. Hence all subsequent references to 'Langebaanweg' refer solely to 'E' Quarry.

Two local faunas are recognized in the Varswater Formation at Langebaanweg but the earlier, from the Quartzose Sand Member, is of similar faunal composition to the later local fauna from the superjacent Pelletal Phosphorite Member. Summaries of the local faunas and geology of the Langebaanweg locality have been published (Hendey 1974, 1976*a*; Tankard 1975) as have detailed descriptions of some of the faunal elements (Maglio & Hendey 1970; Hendey 1972; Hendey & Repenning 1972; Hooijer 1972). The fossiliferous sediments cannot be dated by radiometric methods and, though the fossiliferous

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horizons are associated with a marine transgression, chronological evidence from marine invertebrate faunas has so far proved inconclusive (Hendey, pers. comm.).

The Langebaanweg local faunas include a number of exotic taxa unrepresented elsewhere in Africa (Hendey 1972; Hendey & Repenning 1972; Hendey 1976*b*), but other elements of the fauna may, when studied in detail, afford the best means of gauging the age of the Langebaanweg deposits relative to other fossil mammal localities. The Langebaanweg rhinoceros (Hooijer 1972) suggests chronological equivalence with east African sites dated at or more than 4 m.y. Elephantid remains from 'E' Quarry suggest equivalence with Mursi and Kanapoi (Maglio 1973: 73; Maglio & Hendey 1970). Available evidence from the Langebaanweg Suinae suggests an age of between 4 and 5 m.y. (Harris & White, in preparation). The Langebaanweg giraffoids tend to support these interpretations and the *Sivatherium* appears more primitive than other African occurrences of this genus. It will be interesting to see in due course the relative ages suggested by other mammalian groups.

All specimens referred to in the text or tables with the prefix L are from 'E' Quarry, Langebaanweg. The full prefix for such specimens is SAM–PQ–L.

All measurements given in Tables 1–10 are in millimetres.

SYSTEMATICS

Superfamily GIRAFFOIDEA Simpson, 1931

Following his study of the Miocene giraffoids from east and north Africa, Hamilton (1973) extracted the sivatheres from the family Giraffidae and placed them into a new family Sivatheriidae. His interpretation that the family Giraffidae included only two subfamilies—the Paleotraginae and Giraffinae—is followed here. Two giraffoid species are recognized from Langebaanweg—a sivatheriid represented by nearly 200 specimens and a giraffine represented by over 80 specimens.

Family **Sivatheriidae** Hamilton, 1973

Six sivatheriid genera are recognized from Eurasia and Africa and may be readily distinguished by their ossicone morphology. The frontal bones of *Prolibytherium*, a genus restricted to the early Miocene of north Africa, support large aliform ossicones that have anterior and posterior palmations (Hamilton 1973). *Helladotherium*, known from the early Pliocene of Eurasia (and questionably recorded from north Africa), apparently lacks ossicones and may indeed be a female of *Hydaspitherium* or *Bramatherium* (Matthew 1929; Colbert 1935). *Hydaspitherium*, from the middle Pliocene of Asia, is a gigantic sivatheriid with two ossicones fused at their base into one solid mass on the frontoparietal region (Colbert 1935). *Birgerbohlinea*, from the early Pliocene of Spain, possesses two rounded vertical ossicones that are also strongly connected at their base (Crusafont 1952). *Bramatherium* from the middle Pliocene of Asia has four ossicones

—a large pair growing upward from the frontoparietal region and a smaller pair extending laterally from the parietals (Colbert 1935). Male specimens of *Sivatherium giganteum* from the late Pliocene and Pleistocene of Asia also possess two pairs of ossicones—a small pair arising from the frontal region and a larger pair extending nearly vertically from the parietal region. It is clear from both ossicone and dental morphology that the Pliocene and Pleistocene sivatheriids from Africa are more closely related to *Sivatherium* than to other Eurasian genera and their consequent allocation to this genus seems justified.

Sivatherium Falconer & Cautley, 1835

A diagnosis of this genus is given in Harris (1976). Previously recorded specimens of African sivatheriids exhibit a number of differences from the Asian genotype *Sivatherium giganteum*. Only one relatively complete cranium is known from Africa. This specimen, from the Pleistocene of northern Kenya (Harris 1976), differs from *S. giganteum* in having a longer facial region and a narrower and less deep cranial region. The posterior ossicones of recorded African sivatheriids are orientated differently from the Asian species and the anterior ossicones, if interpreted as such, are sited more posteriorly and are less prominently developed (Harris 1974). The teeth of Asian and African *Sivatherium* specimens are, however, similar in morphology. Nevertheless the cranial differences, and particularly those of the ossicones, are sufficient to warrant taxonomic separation from *S. giganteum*.

Owing to the fragmentary nature of much of the material, a number of difficulties are encountered in attempting to identify African sivatheriids to species level. In their monograph on the fossil giraffoids of Africa, Singer & Boné (1960) recognized six different taxa:

Libytherium maurusium
Sivatherium olduvaiense
S. olduvaiense haughtoni
S. olduvaiense vanhoepeni
S. olduvaiense subsp. indet.
Sivatherium cingulatum

As subsequently noted (Churcher 1974; Harris 1974), the type mandible of *L. maurusium* was found by Arambourg (1960) to have been wrongly restored. Arambourg's new restoration clearly showed that *L. maurusium* and *S. olduvaiense* were conspecific and that the common African sivathere should be called *Sivatherium maurusium*.

With regard to the other taxa recognized by Singer & Boné (1960) it is evident that the type (and only) upper molar of *S. cingulatum*, the type (and only) lower molar fragment of *S. olduvaiense haughtoni*, the four incomplete teeth from Tierfontein assigned to *S. olduvaiense* subsp. indet. and an incomplete lower molar from Florisbad assigned to *S. olduvaiense* are all larger than the range of variation exhibited by other specimens assigned to *S. maurusium*.

Tierfontein, Florisbad and Cornelia are all middle to late Pleistocene sites and the provenance of the other large specimens is poorly substantiated other than that they come from the 'Vaal River Gravels'. It is entirely possible that these large teeth from the Orange Free State and the Cape Province are from late South African representatives of *S. maurusium*, especially as the ossicones from Tierfontein may unequivocally be assigned to this species. If so, then nearly all the African sivatheriids reported to date can be assigned, or at least referred, to a single species.

South African material that is more directly comparable to east and north African specimens of *S. maurusium* has been collected from Elandsfontein (Singer & Boné 1960). The Elandsfontein material includes deciduous and permanent teeth, posterior ossicones and metapodials. A few deciduous and permanent teeth are known from Makapansgat but, in the absence of ossicones from that site, cannot be identified to species. A single unerupted *Sivatherium* molar is also known from Swartkrans (Churcher 1974).

There is currently no evidence to support more than one species of *Sivatherium* from Langebaanweg. If an early Pliocene age is corroborated by subsequent investigation of other fossil mammals from that locality the Langebaanweg *Sivatherium* would appear to be the earliest record of the genus. The sivathere from this locality possesses conical anterior ossicones that are present also in the Asian species but absent in *S. maurusium*. The posterior ossicones of the Langebaanweg form are not, however, palmate and near-vertically orientated as in *S. giganteum*, but extend backwards and outwards from the cranium as in the common morph of *S. maurusium* (Type A of Harris 1974). Several posterior ossicones are known from Langebaanweg and all may be distinguished from those of *S. maurusium* by their lack of ornamentation in terms of knobs and flanges.

African *Sivatherium* ossicones are quite variable in morphology although all apparently conform to one of three basic shapes (Harris 1974). The ossicones are present only in male specimens and the degree of ornamentation may well be a function of the age of the individual (cf. secondary bone apposition in extant male giraffes). It is possible therefore that the Langebaanweg sivathere ossicones, like those of the Langebaanweg giraffines, are all from immature individuals. On balance, however, the erection of a new species for the Langebaanweg sivathere appears warranted on morphological grounds.

Sivatherium hendeyi sp. nov.

Figs 1–7

Sivatherium olduvaiense (Hopwood): Singer & Boné, 1960: 544–5.
Libytherium olduvaiense (Hopwood): Hendey, 1970: 98.

Holotype

SAM–PQ–L12730, virtually complete left ossicone from the Quartzose Sand Member of the Varswater Formation in 'E' Quarry, Langebaanweg.

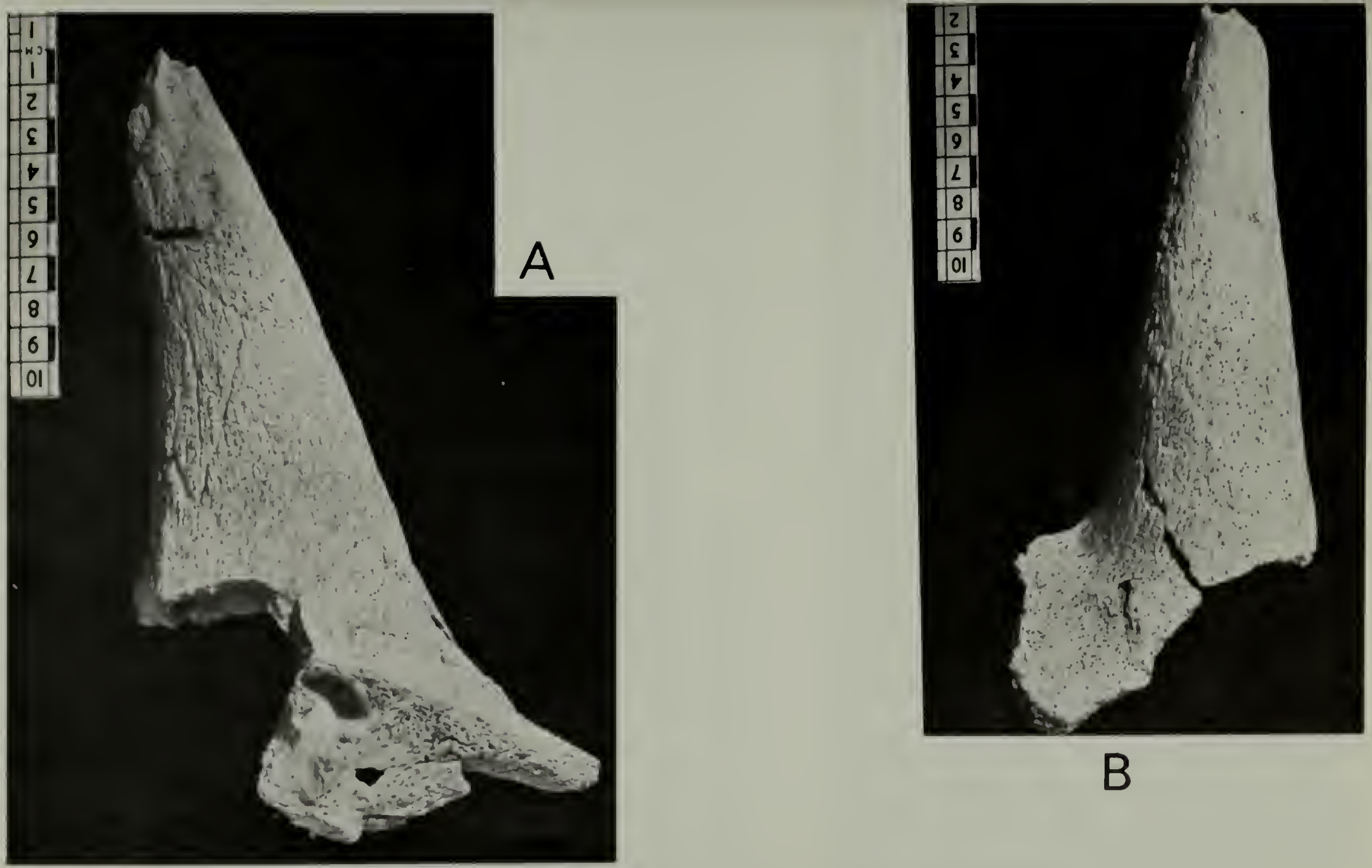

Fig. 1. *Sivatherium hendeyi* left anterior ossiocone (SAM–PQ–L31285, paratype).
A. Medial view. B. Anterior view.

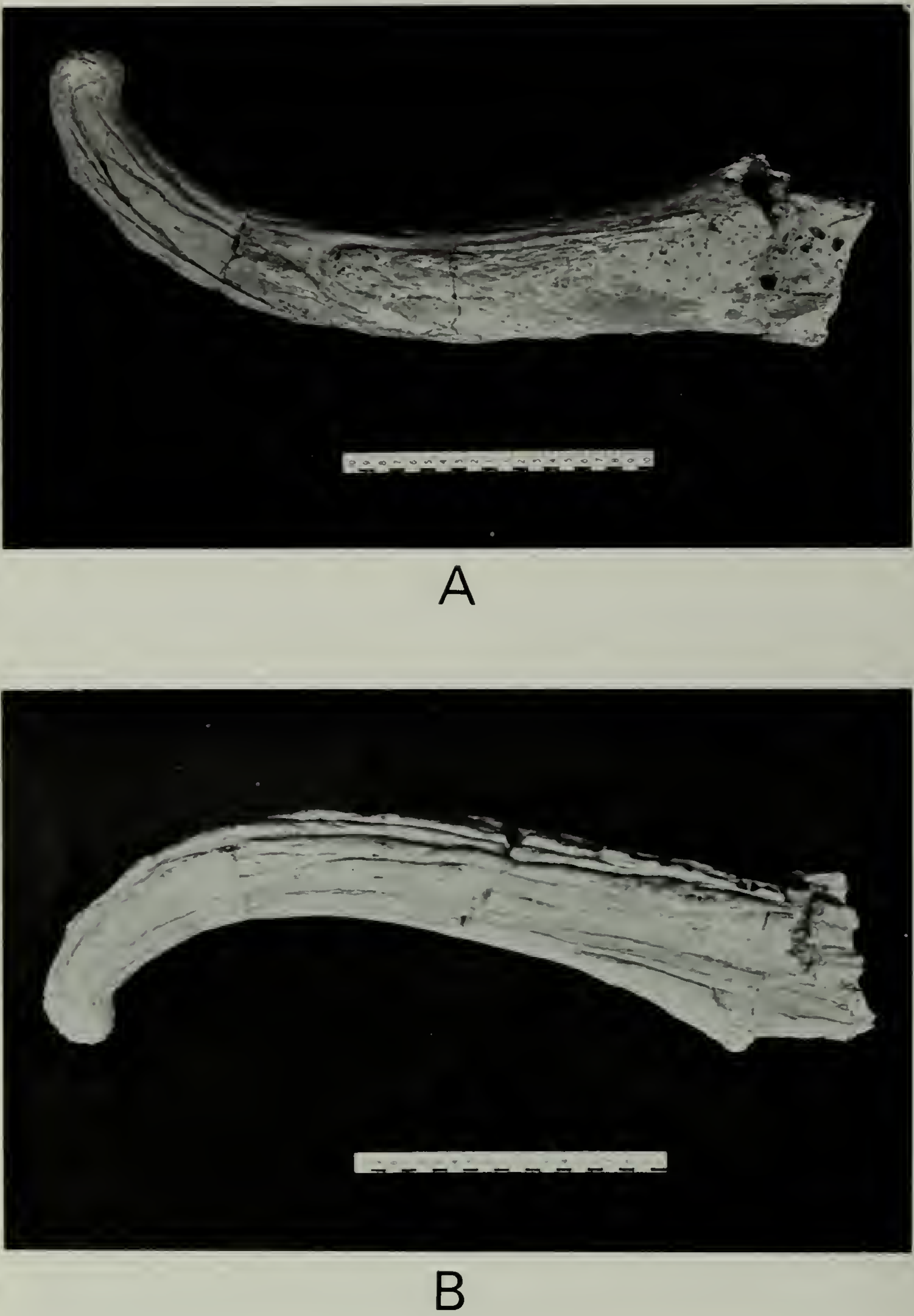

Fig. 2. *Sivatherium hendeyi* left posterior ossicone (SAM–PQ–L12730, holotype). A. Ventral view. B. Dorsal view.

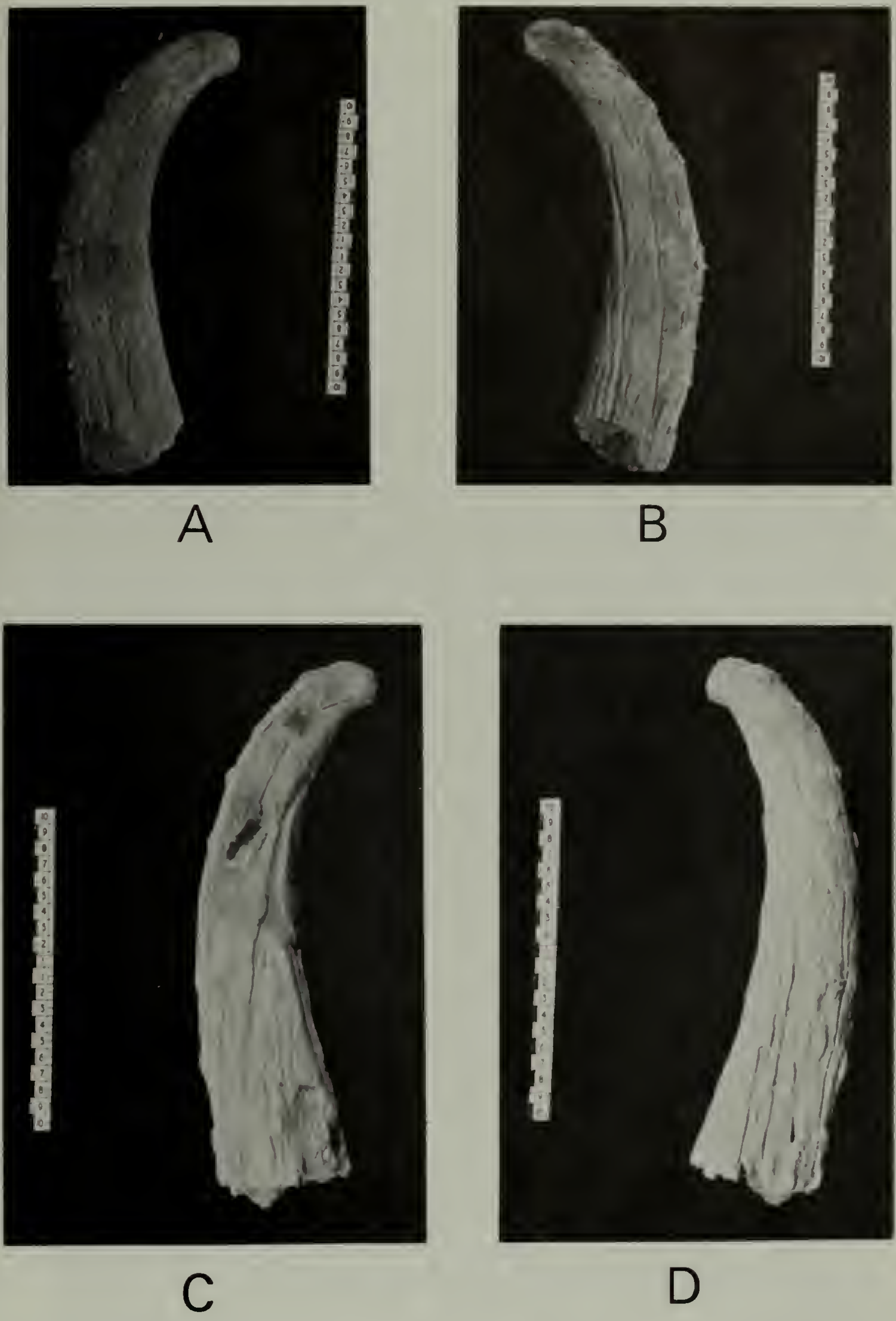

Fig. 3. *Sivatherium hendeyi* incomplete posterior ossiocones.

A. SAM–PQ–L7243, right posterior ossicone, dorsal view.
B. SAM–PQ–L7243, right posterior ossicone, ventral view.
C. SAM–PQ–L7244, left posterior ossicone, ventral view.
D. SAM–PQ–L7244, left posterior ossicone, dorsal view.

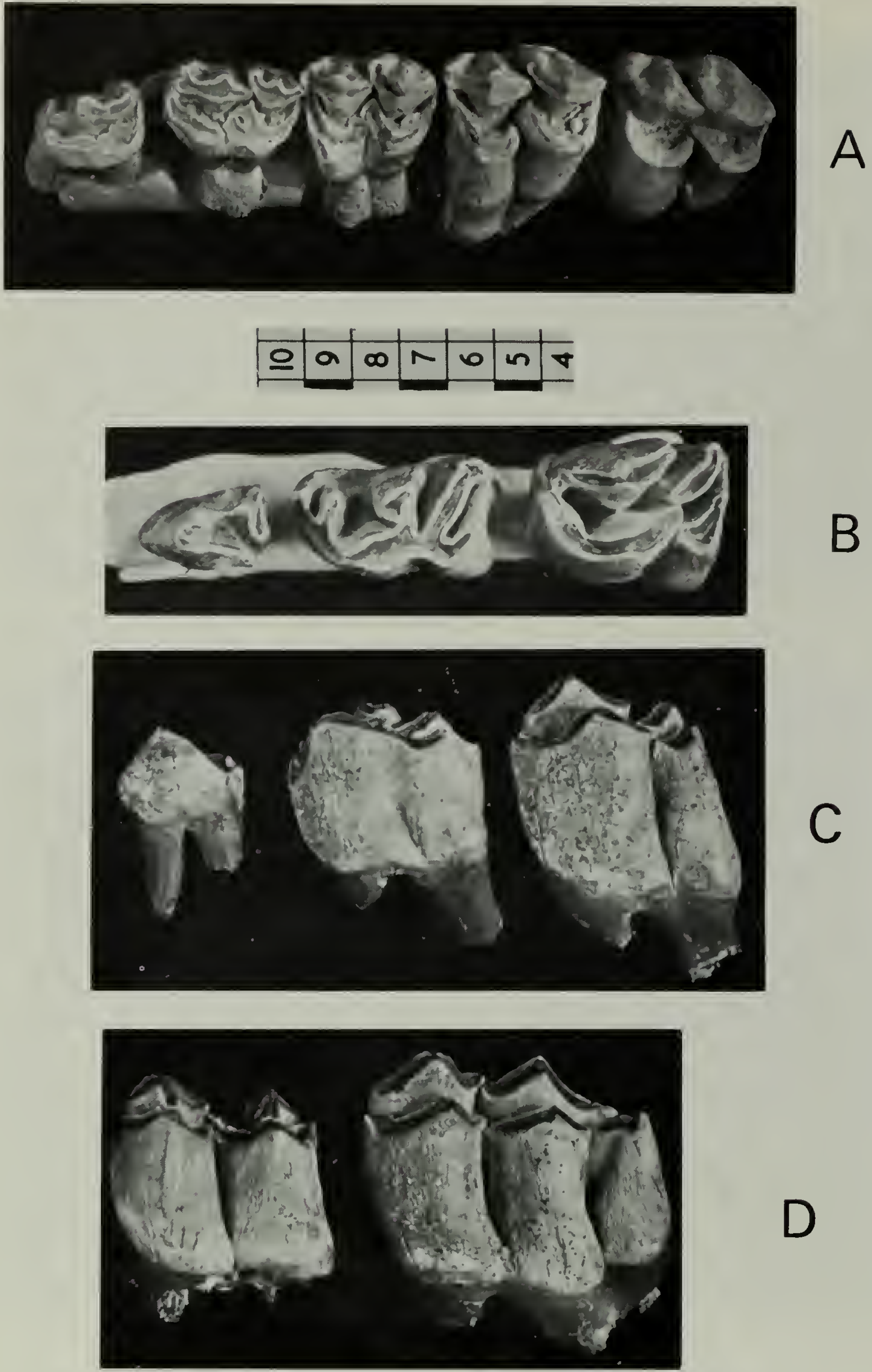

Fig. 4. Giraffoid dentitions from 'E' Quarry, Langebaanweg.
A. SAM–PQ–L10343, *Giraffa* cf. *G. jumae* upper dentition (LDP^2–M^2), occlusal view. B. SAM–PQ–L31137, *Sivatherium hendeyi* lower dentition (LP$_{2-4}$), occlusal view. C. SAM–PQ–L31137, *Sivatherium hendeyi* lower dentition (LP$_{2-.4}$), lateral view. D. SAM–PQ–L31137, *Sivatherium hendeyi* lower dentition (LM$_1$, LM$_3$), lateral view.

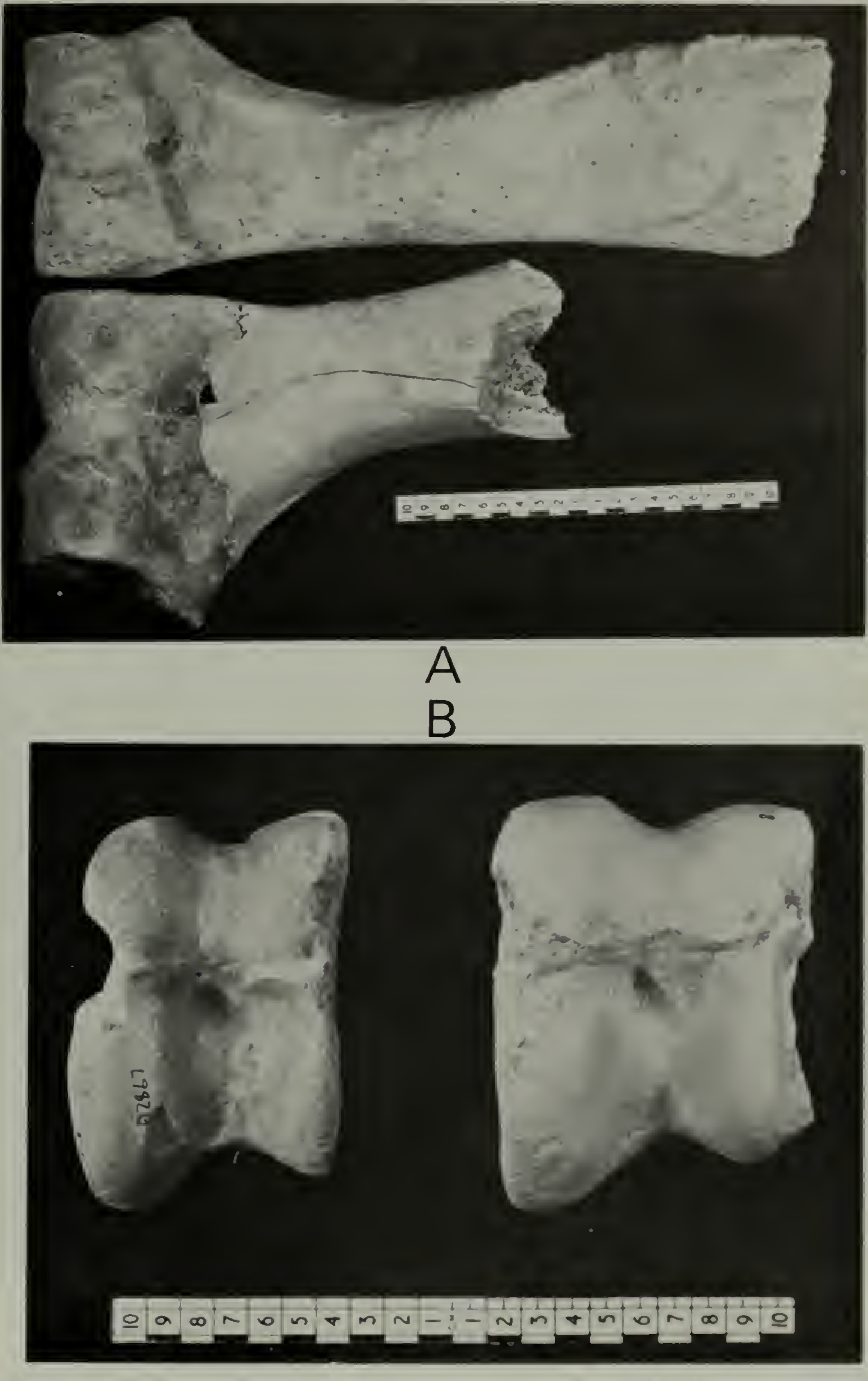

Fig. 5. Giraffoid postcranial elements from Langebaanweg.
A. Distal humeri of *Giraffa* cf. *G. jumae* (top) and *Sivatherium hendeyi* (bottom), anterior view.
B. Left astragali of *Giraffa* cf. *G. jumae* (left) and *Sivatherium hendeyi* (right), anterior view.

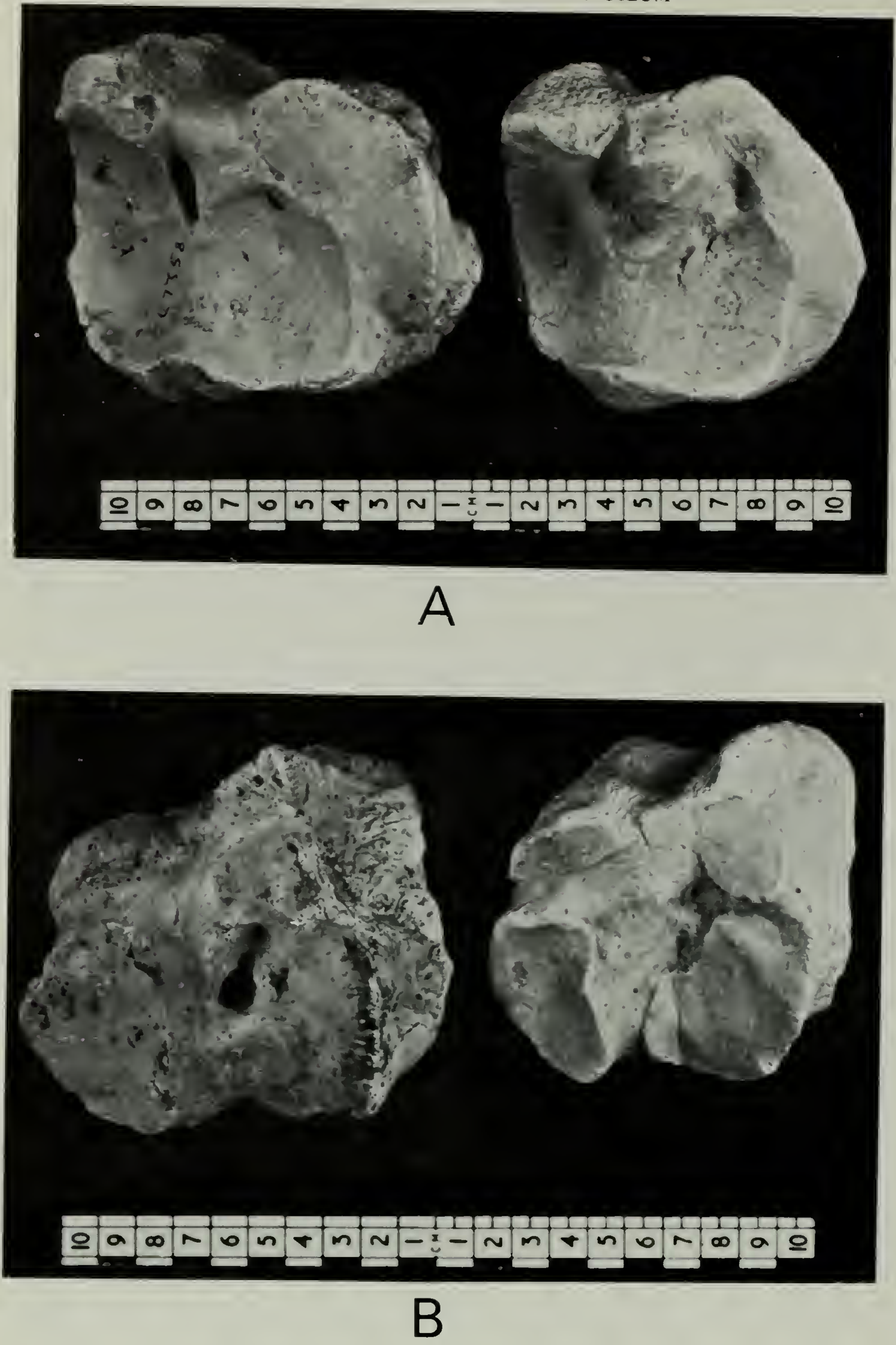

Fig. 6. Giraffoid naviculocuboids from Langebaanweg.
A. Left naviculocuboids of *Sivatherium hendeyi* (left) and *Giraffa* cf. *G jumae* (right), proximal view. B. left naviculocuboids of *Sivatherium hendeyi* (left) and *Giraffa* cf. *G. jumae* (right), distal view.

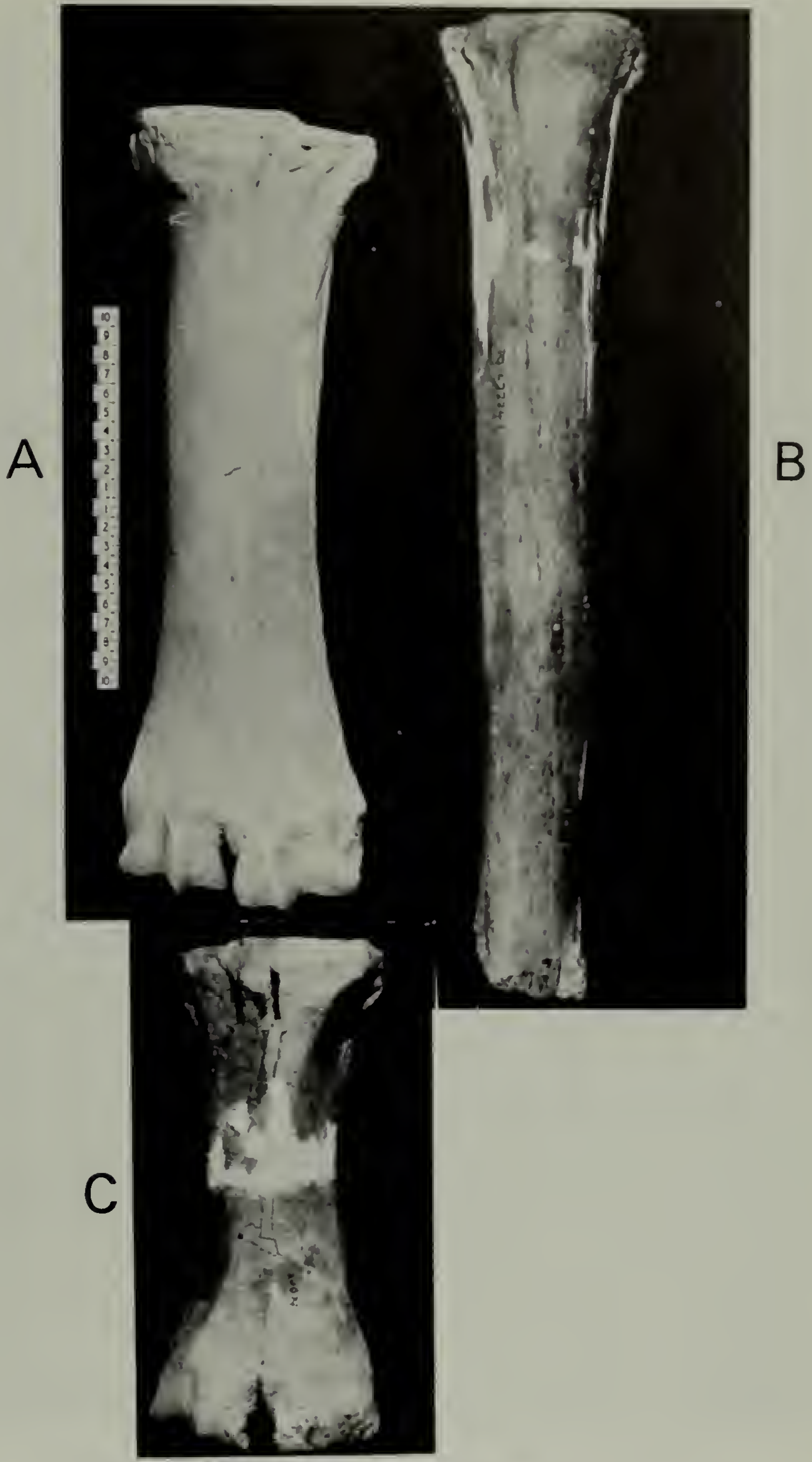

Fig. 7. Giraffoid metacarpals.

A. Left metacarpal of *Sivatherium hendeyi* from Langebaanweg, anterior view. B. Proximal right metacarpal of *Giraffa* cf. *G. jumae* from Langebaanweg, anterior view. C. Right metacarpal of *Sivatherium maurusium* from Elandsfontein, anterior view.

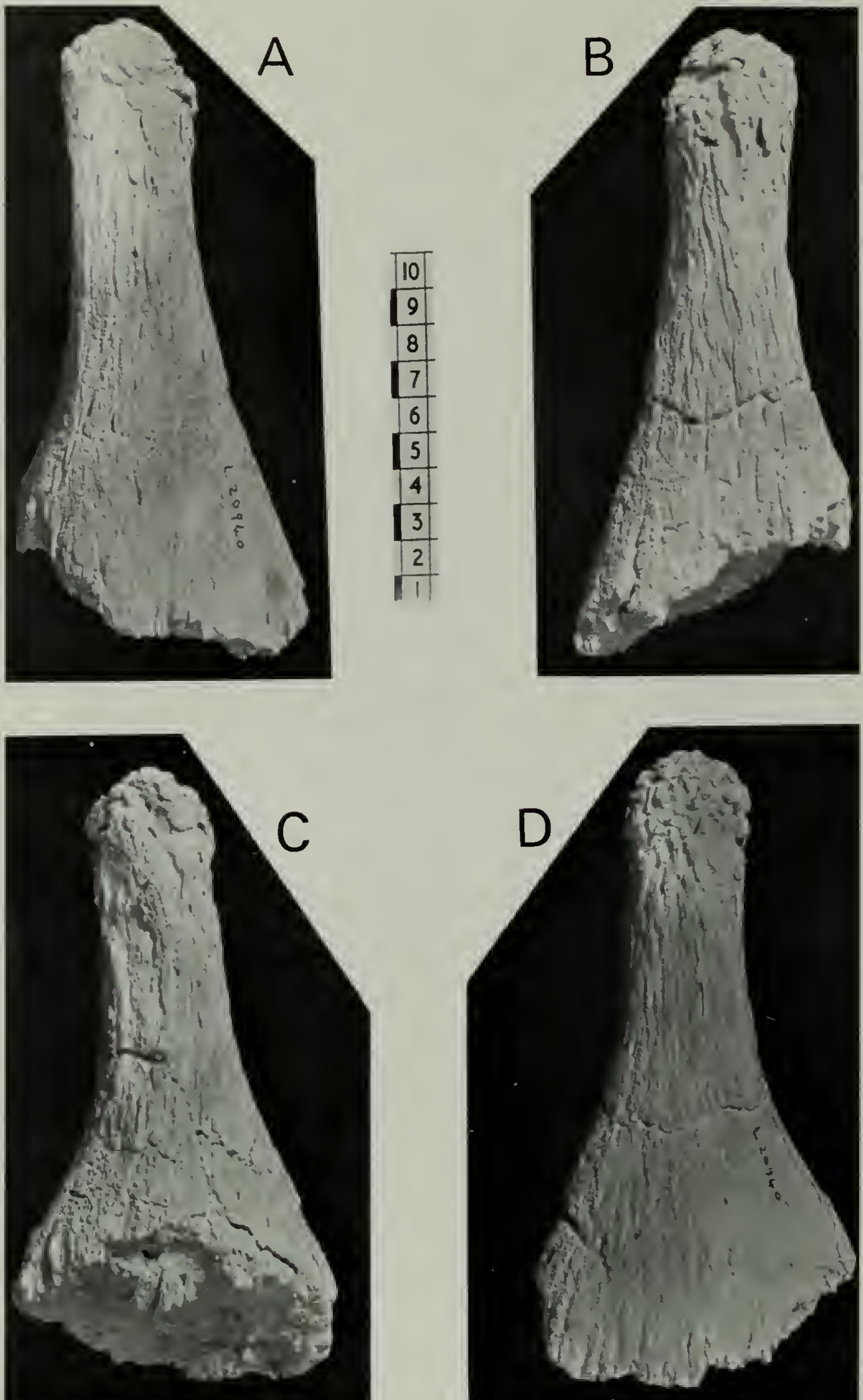

Fig. 8. Ossicones of *Giraffa* cf. *G. jumae* from Langebaanweg.
A. SAM–PQ–L20490, *Giraffa* cf. *G. jumae* left ossicone, medial view. B. SAM–PQ–L20940, *Giraffa* cf. *G. jumae* left ossiocone, lateral view. C. SAM–PQ–L20940, *Giraffa* cf. *G. jumae* right ossicone, lateral view. D. SAM–PQ–L20490, *Giraffa* cf. *G. jumae* right ossicone, medial view.

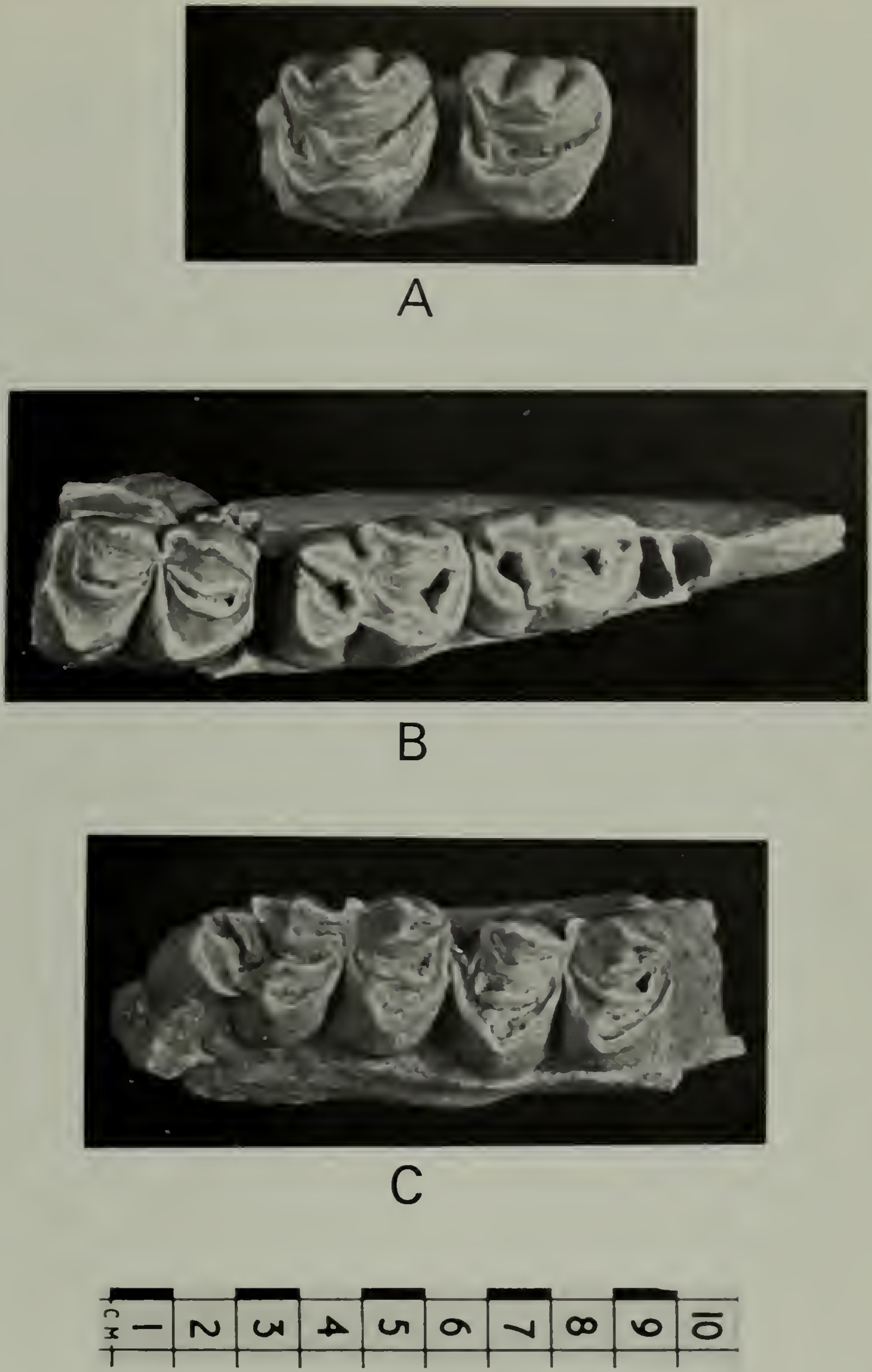

Fig. 9. Teeth of *Giraffa* cf. *G. jumae* from Langebaanweg.

A. SAM-PQ-L30126, *Giraffa* cf. *G. jumae* upper premolars (RP^{3-4}), occlusal view. B. SAM-PQ-L31138, *Giraffa* cf. *G. jumae* partial right mandible (RP_3–M_1), occlusal view. C. SAM-PQ-L31138, *Giraffa* cf. *G. jumae* partial right mandible (M_{2-3}), occlusal view.

Paratype

SAM–PQ–L31285, right and left anterior ossicones from the Pelletal Phosphorite Member of the Varswater Formation in 'E' Quarry, Langebaanweg.

Diagnosis

Species of *Sivatherium* of similar size and dental morphology to *S. giganteum* and *S. maurusium*. Posterior ossicones short, extending laterally and backwards from the cranium and unornamented by knobs and flanges or palmate digitations. Anterior ossicones conical as in *S. giganteum*. Metacarpals longer than in other species of *Sivatherium*.

Etymology

The species is named after Q. B. Hendey, who has been responsible for collecting most of the 'E' Quarry Langebaanweg fauna.

Cranial material

Anterior ossicones

A single pair of anterior ossicones (L31285) has been recovered from the Pelletal Phosphorite Member at Langebaanweg. The left anterior ossicone lacks its distal tip but the base of the ossicone is complete and, on the medial side, extends as far as the intrafrontal suture. The right ossicone is broken distally and the lateral portion of the base is also missing.

The anterior ossicones are conical structures, as in *S. giganteum*, and are slightly compressed mediolaterally (the lateral side being the flatter). They are inclined backwards at an angle of 50° to the cranial vault at the intrafrontal suture. They also diverge outwards from each other. A large basal sinus is present and the adjoining frontal bone is cancellous. The anterior and lateral surfaces of the anterior ossicones are relatively smooth but a number of irregular longitudinal ridges and furrows are present on the posterior surface though less prominent than the grooves on the posterior ossicones.

The anterior ossicones from Langebaanweg would appear to be the first unequivocal specimens from an African sivathere. Anterior ossicones have previously been reported from Tierfontein and Elandsfontein (Singer & Boné 1960, pls 29, 42) but the Tierfontein specimen is almost certainly part of a posterior ossicone while the Elandsfontein specimen is unfortunately no longer available for examination. The similarity of the conical anterior ossicones to those of *Sivatherium giganteum* confirm the relationship of the Pliocene African sivatheres with *Sivatherium* from Asia. Anterior ossicones are not present in the relatively complete sivathere skull from Koobi Fora, Kenya (Harris 1976), and the apparent absence of anterior ossicones from other later Pliocene and Pleistocene accumulations suggests that they are greatly reduced or lost in *S. maurusium*.

Posterior ossicones

No complete posterior ossicone is known from Langebaanweg although L12730 is virtually complete and apparently lacks only a few centimetres of bone from its junction with the cranial vault. Other less complete specimens include L2542 (right ossicone fragment), L3690 (dorsal fragment of proximal right ossicone), L4083 (ventral fragment proximal right ossicone), L7243 (distal right ossicone), L7244 (distal left ossicone), L7245 (posterior fragment of proximal right ossicone), L7246 (fragment of proximal ossicone) and L6247 (fragment of proximal left ossicone).

The posterior ossicone morphology is closest to Type A of Harris (1974), extending outwards and backwards from the cranial vault and perhaps slightly upwards at the distal tip. The ossicones exhibit only a faint degree of torsion (anticlockwise in the right ossicone). Near the base each ossicone is almost triangular in transverse section with a flat dorsal surface and a strongly convex ventral surface. The distal third is more rounded and is almost circular in transverse section. The posterior and ventral surfaces are smooth for almost their entire length. The anterior and dorsal surfaces are sculpted by deep and wide longitudinal grooves that through torsion extend on to the ventral surface in the distal portion of the ossicone. The intervening ridges are rugose on the anterior surface of the proximal portion of the ossicones and again at intervals on the distal portion. These rugosities are interpreted to foreshadow the flange and discrete knobs that are a distinctive feature of specimens of *S. maurusium*. The longitudinal grooves of the dorsal surface of the ossicone are less deep and less numerous than those of the anterior surface. Each ossicone terminates in a distinct bulbous knob.

The low degree of torsion, small size, small basal sinus, virtual absence of grooves on the ventral surface and lack of flanges and knobs on the posterior ossicones when taken in conjunction with the discrete conical anterior ossicones serve to distinguish *S. hendeyi* from *S. maurusium*. It is likely, none the less, that the latter evolved from the former.

Dentition

Although a couple of reasonably complete lower dentitions are known, most of the Langebaanweg sivathere teeth comprise isolated specimens. The more complete specimens are listed in the tables of dental measurements (Tables 2–4). The teeth of *S. hendeyi* are morphologically indistinguishable from those of *S. maurusium* and are of similar size to the *S. maurusium* teeth from the near-by but later locality of Elandsfontein. The Elandsfontein and Langebaanweg sivathere teeth are larger than those from Makapansgat but smaller than comparable specimens from the Vaal River localities.

Postcranial material

A large number of giraffoid postcranial elements have been recovered from the Varswater Formation. The apparent presence of only one giraffine and one sivatheriid species and the occurrence of associated skeletal elements permit ready identification of *Sivatherium* versus *Giraffa* postcranial elements. Accession numbers of *Sivatherium* limb bones are given in the tables of measurements. Observed differences between the Langebaanweg sivatheriid and giraffine skeletal elements are listed below.

Scapula

It is difficult if not impossible to separate scapulae of *Sivatherium* from those of *Giraffa* solely on fragments of the glenoid. Specimens larger than those of extant *G. camelopardalis* almost certainly belong to *Sivatherium* but smaller specimens may represent either *Giraffa* or immature *Sivatherium* individuals. The posterior border of the blade is distinctly more rounded in *Sivatherium*, but this feature can be used only for the more complete specimens which, by virtue of the relative fragility of the blade, are rare in the fossil record.

Humerus

No complete or proximal giraffoid humeri are known from Langebaanweg but several distal epiphyses, some with distal portions of the shaft, have been collected. *Sivatherium* humeri tend to be larger in overall size and with shorter but relatively more massive diaphyses than those of giraffines. The distal portion of the shaft widens to meet the lateral epicondyle more rapidly than in *Giraffa*. The coronoid fossa is smaller and less deep in *Sivatherium*. The posterior articular surface of the lateral condyle is smaller in *Sivatherium* and the area for attachment of the extensor digitalis communis is larger.

Ulna

The semilunar notch of the *Sivatherium* ulna is proportionately larger and wider than in Giraffa. It is divided into two unequal halves by a low ridge but, unlike in *Giraffa*, the lateral portion is larger than the medial. The semilunar notch extends for the entire width of the ulna in *Sivatherium* but not in *Giraffa*. Distal to the semilunar notch the lateral facet for articulation with the radius is much shorter in *Giraffa*.

Radius

The radius of *Sivatherium* is proportionately shorter and less straight than that of *Giraffa* although more massive. The notch dividing the medial from the lateral facet in the proximal epiphysis extends for nearly half the craniocaudal length of the epiphysis in *Sivatherium* but is much shorter in *Giraffa*. The distal epiphysis is of similar morphology to that of *Giraffa* but is wider laterally. On the caudal edge of the distal epiphysis the articular facets extend farther proximally but the styloid process of the ulna extends less far posteriorly in *Sivatherium* than in *Giraffa*.

Metacarpals

Sivatherium metacarpals closely resemble those of *Giraffa* but are shorter, wider and with larger epiphyses. Most specimens from Langebaanweg comprise either proximal or distal epiphyses. The distal epiphysis of the sivathere metacarpal may be distinguished from that of *Giraffa* by its larger size and proportionately wider epiphyseal region. Proximal epiphyses may be separated by the same factors but, in addition, the lateral facet of the proximal epiphysis is normally less widely separated from the medial facet at its posterior edge in *Giraffa*. The shaft of the sivathere metacarpal is proportionately less deep craniocaudally.

Tibia

Sivatherium tibiae are shorter but proportionately more massive than those of giraffine species. The proximal epiphysis is of similar width to that of *Giraffa* but is relatively longer craniocaudally. The cnemal crest, extending distally from the proximal epiphysis, is stout and extends nearly half-way down the shaft. In *Giraffa* the cnemal crest is less prominent and is confined to the proximal third of the shaft. Moreover the central and distal portions of the shaft are more craniocaudally compressed in *Giraffa*. In the distal epiphysis the articular facets for the fibula are more horizontally aligned in *Sivatherium*, those of giraffine tibiae being inclined more steeply towards the lateral edge of the epiphysis.

Fibula

Sivatherium fibulae are rather smaller in overall size than those of *Giraffa* and the tibial facets are less wide, less elongate and have greater relief. The anterior tibial facet is convex rather than flat as in *Giraffa* and is inclined laterally at a less steep angle. The process on the dorsal edge of the sivathere fibula is both less tall and less massive than that of *Giraffa*. The posterior tibial facet of the *Giraffa* fibula extends farther forwards towards the lateral edge. The calcaneal facet on the ventral surface of the fibula is both more elongate anteroposteriorly and more concave in *Sivatherium*.

Calcaneum

Sivathere and giraffine calcanea are difficult to separate. Even with the aid of associated skeletal material of known genus, only one minor morphological feature serves to distinguish the two. Both *Sivatherium* and *Giraffa* calcanea have an elongate anteroventral facet on the inferior surface for articulation with the naviculocuboid. In *Giraffa* the posteromedial edge of the naviculocuboid facet extends dorsally on to the medial side of the anterior process of the calcaneum. The additional facet is apparently absent from *Sivatherium* calcanea.

Astragalus

Sivathere and giraffine astragali are very similar in morphology. Sivathere astragali tend to be larger in fully adult specimens. The only morphological feature serving to differentiate the two genera is that *Sivatherium* lacks the lateral notch that in *Giraffa* is present between the tibial trochlea and naviculocuboid trochlea. The validity of this distinguishing feature is questionable, for the lateral notch tends to be at least partly infilled in mature male specimens of *G. camelopardalis*.

Naviculocuboid

The *Sivatherium* naviculocuboid tends to be larger than that of *Giraffa*. On the dorsal (proximal) surface the articular facet for the calcaneum often extends farther posteriorly in *Giraffa*. The two articular facets for the astragalus are more markedly separated at their posterior edge in *Sivatherium* and the posterior edge of the lateral astragalus facet is not raised dorsally as in *Giraffa*. On the ventral (distal) surface the metatarsal facet is proportionately larger than that of *Giraffa* but giraffine naviculocuboids possess an additional transversely orientated facet for articulation with the posterior edge of the metatarsal and which is absent in *Sivatherium*.

Metatarsal

The *Sivatherium* metatarsal is shorter, wider and more massive than that of *Giraffa*. The proximal epiphyses differ slightly to reflect the different morphology of the distal naviculocuboid and, in addition, are larger in *Sivatherium*.

Remarks

Certain trends are evident in the evolution of African sivatheriid ossicones. These include reduction (and perhaps posterior migration) of the anterior ossicones, elongation and increase in torsion of the posterior ossicones, development of secondary bone apposition on the anterior edges of the posterior ossicones and increase in size of the basal sinus concomitant with increase in overall size.

The common morph of the posterior ossicones of *S. maurusium* (Type A of Harris 1974) could clearly have evolved from the condition seen in *S. hendeyi*. So far different morphs of *S. maurusium* ossicones (Types B and C of Harris 1974) have been recorded only from Bed II at Olduvai, but each morph is represented by several individuals. It is possible that the different ossicone shapes seen at Olduvai are indicative only that the ossicones of *S. maurusium* were variable and they thus have no taxonomic significance. It is, however, also possible that the African sivatheriids were as diverse as those from Asia and, as in some bovid tribes, specific differences are more immediately evident from the cornual protuberances than from other parts of the body. This question can be resolved only after the collection of further and more complete cranial material from different localities.

Another apparent evolutionary trend is seen in the metacarpals, those of *S. hendeyi* being longer than those of *S. maurusium* and *S. giganteum*. Metacarpals of *S. maurusium* appear to decrease in length through time. Shortening of the metatarsals is less marked and no pronounced trends have been observed in other elements of the skeleton or in the teeth.

TABLE 1

Measurements of *Sivatherium hendeyi* ossicones

	L12730 (posterior)	L31285 (anterior)
Length	450+	195+
Basal diameter ap	120	94
Basal diameter dv	92	
Basal diameter tr		71

TABLE 2

Measurements of *Sivatherium hendeyi* deciduous teeth

	L2047	L2048	L2049	L2358	L13051	L30475	L2540	L10179	L10809	L13315
DP^2 ap			35,9′							
tr			28,7′							
DP^3 ap		36,7			33,9					
tr		31,2			31,6					
DP^4 ap	38,5*			37,5	—					
tr	39,3			39,3	40,0					
DP_3 ap									35,8	32,6
tr									19,7	20,4
DP_4 ap							44,1	51,5		
tr							24,8	29,0		

TABLE 3

Measurements of *Sivatherium hendeyi* upper teeth

	L1865	L1873	L2046	L11352A	L12083
P^3 ap		32,9			
tr		44,5			
P^4 ap	34,2				
tr	41,5				
M^1 ap			47,6*		
tr			51,6		
M^2 ap					53,2
tr					54,2
M^3 ap				51,9	
tr				49,4	

TABLE 4

Measurements of *Sivatherium hendeyi* lower teeth

	L1839	L1876	L3468	L5468	L7247	L7248	L7249	L9161	L9163	L30875	L31137
P_2 ap											27,5
tr											17,4
P_3 ap						37,9		38,9			39,7
tr						28,5		27,1			26,3
P_4 ap				43,5	40,7		40,6	42,5			44,5
tr				31,5	28,2		28,5	29,3			31,9
M_1 ap		45,5	44,3					46,1		47,2	44,4
tr		32,4	34,4					30,6		35,0	33,8
M_2 ap								50,6	52,2		
tr								36,7	36,7		
M_3 ap	74,5′							71,5			64,2
tr	38,1′							34,7			33,1

Table 5

Measurements of *Sivatherium hendeyi* postcranial elements

SCAPULA	L20141	L3093	L22281	L20949	L1272	L12742					
Max length blade	600+										
Max width articular edge	141	164	177	162+	162	149					
Max width glenoid	91	97	127	120+	127	113					
Max depth glenoid	85		118		102	102					
HUMERUS	L3096	L2239	L3097	L3434	L8897	L12377	L6883	L21569			
Width lat epicondyle	187		149	187	167			133			
Width distal epiphysis	169				153		161	121			
Depth distal epiphysis	106				96*	116	102				
ULNA	L2242	L2243	L3112	L6036	L8069						
Depth olecranon ap (at junction of epiphysis)	115+	97	94+	100							
Width humerus facet tr	78	85			86						
Depth humerus facet ap	63	62	58	60	73						
RADIUS	L21569	L2240	L2241	L22139	L9813	L12844	L14355	L14177			
Length	625										
Proximal epiphysis tr	164	165		160							
ap	82	89		80				86			
Distal epiphysis tr	137		143			114	129				
ap	87		82		72	74	82				
METACARPAL	L4746	L20195	L3114	L14173	L19844	L12088	L9842	L7261	L4958	L7263	L20796
Length	350	400	415	390							
Proximal epiphysis ap	68	80	88	81	74		71			71	79
tr	100	108		121	109		108			74	113
Distal epiphysis ap	58	66	74	70		70		62	60		
tr	100	111	123	119		117		115	110		
	L6219	L5704	L12052B	L12742	L9843	L20860	L11864	L20240	L14174	L2245	L3111
Proximal epiphysis ap				78	72	71	80				
tr				108	106	115	113				
Distal epiphysis ap	68	63					65+	61	62	60	59+
tr	110	107					114	109	110	110	110+

TABLE 5 (*continued*)

TIBIA	L22186	L5420	L13972	L14244									
Length	580	530											
Proximal epiphysis ap													
tr	163	169											
Distal epiphysis ap	88	81	73	83									
tr	127	122	102	125									
FIBULA	L6096	L6097											
Max length ap	62	63											
Max breadth tr	36	36											
Max height dv	51	46											
CALCANEUM	L5399	L5896	L6334	L3106	L13970	L12658							
Length	210	219	208	200	225								
Width articular region	86	90	87		101								
Depth articular region	95	102	92	93	100	101							
Width tuber calcis	64	67	62		62								
Depth tuber calcis	72	74	63		66								
ASTRAGALUS	L7391	L7385	L7390	L25032	L12393	L7378	L7384	L12657	L3259	L7392	L7376	L4222	
Lat length	128				119	111	129	127	129	129		125	
Med length	114	106	102				109	104	117	109	109	106	
Width tibial trochlea	92						88	82	85+	83	84	77	
Width navcbd trochlea	84	75		73				82	90	84	81	81	
Depth ap	68	69	65	66	58			70′	82				
	L7393	L7381	L7382	L7387	L7377	L7378	L9827	L3550	L20853	L6207	L12745	L6028	L3094
Lat length	126				123	126		127	123	125		132	126
Med length	112	106	108	113	109	109	109	103	108	109	101	112	102
Tibial tr	93	80	76	98	86	85		87	93	94	87	92	85
Navcbd tr	86				76	83	79	81	83	87	83	84	80
Depth ap	74	64	70	78	69			68	75	74	72	76	
	L21820	L9830	L1242	L9829	L3092	L2238	L20851	L2233	L1263	L20242	L4233	L6027	L11753
Lat length		121	94	117	126	118	125	128	132	129	130	123	123
Med length	99	110	84	101	106	101	106	106	110	111	113	103	106
Tibial tr	91	90	67	86	77	87	87	81	88	87	95	88	93
Navcbd tr	79	82	64		81	87	79	79	80	87	79	75	81
Depth ap	69	69	55	69		73	72	70	76	75	71	74	72

TABLE 5 (*continued*)

NAVICULOCUBOID	L3109	L1800	L7632	L13679	L7896	L6029	L7406	L4229	L7359	L3798	L9219	L5157
Median length ap . .	99	104	113			108		112	108	107	94	99
Max width	102	108	114		100	112	97	106	95	106	103	98
Lateral depth dv . .	57	57	58	56	57	60	57	58	56	55	54	54

NAVICULOCUBOID	L14712	L4230	L7538	L11906	L12614	L14123	L3104	L9835	L2232	L13156	L4231	L4739
Med length	121			96			106	100	95	115	114	87
Max width	118	106	105	89	84	110	106	104	101	105	113	97
Lat height	58	59	57	54	50	65	57	52	57		57	51

METATARSAL	L5401	L20623	L7258	L13971	L12246	L1244	L7259	L12247	L21534	L7262	L9274	L14339	L14145
Length	410												
Proximal ap . . .	89	100	98	66	66	68	68	99				93	85
tr	94	101	99	82		74	101						
Distal ap	58				63			70	63+	63	56		
tr	95				104			111	107	105	95		

Family **Giraffidae** Gray, 1821

According to Hamilton (1973) this family contains only paleotragines and giraffines. *Zarafa* from the early Miocene of north Africa is the earliest representative of the family and was assigned to the Paleotraginae although not on the direct lineage to later giraffines or paleotragines (Hamilton 1973, fig. 13). Giraffines appear to have been of Asian origin but the presence of *Giraffa* in the early Pliocene of South Africa may require some modification of the evolutionary sequence of *Honnanotherium*, *Bohlinia*, *Giraffa*, suggested by Bohlin (1935) and accepted by Hamilton (1973).

Subfamily Giraffinae Zittel, 1893

Three extinct giraffine species have been recognized in the late Pliocene and early Pleistocene localities of east Africa (Harris 1976). The smallest species, *Giraffa pygmaeus*, is known from ossicones and dentitions but postcranial remains have so far proved rare. The other two species, *G. gracilis* and *G. jumae*, are more completely represented in the fossil record although no complete crania have yet been found of *Giraffa gracilis*. The two larger extinct *Giraffa* species may be readily identified on the basis of ossicone morphology and orientation. The teeth and postcranial elements of all giraffine species are, however, very similar in morphology. Both the teeth and postcranial elements of *G. jumae* tend to be larger than those of *G. gracilis*, but owing to size variation and sexual dimorphism neither the teeth nor the skeletal elements of these two species can always be separated with certainty. The same is true of the teeth of *G. pygmaeus* and *G. gracilis* from Pliocene localities. It is unfortunate that so few associated giraffine cranial and postcranial remains have been retrieved to date but, taking into account the fragmentary nature of the Plio-Pleistocene giraffine remains from east Africa, the taxonomic criteria adopted by Harris (1976) appear to be valid.

Giraffa cf. *G. jumae* Leakey, 1965

Figs 4–9

Diagnosis

A diagnosis revising that of Leakey (1965) is given in Harris (1976).

Cranial remains

Ossicones

Only three giraffine ossicones have been retrieved from Langebaanweg. The best preserved specimens comprise a left and right ossicone from a single individual (SAM–PQ–L20940) collected from the Quartzose Sand Member. The individual was immature and neither ossicone had been fused to the cranium. The two ossicones are similar in morphology to, but rather smaller than, those of immature extant male giraffes. The lateral edge of each ossicone base is flat but the medial edge is expanded towards its fellow. Each ossicone tapers gradually above its base but a distinct terminal knob is present at the distal extremity. The posterior surface of the ossicone is slightly concave but the anterior surface is virtually flat, both as in *G. jumae.* The surface of each ossicone is cut by a number of irregular longitudinal grooves that are most pronounced on the anterior and median surfaces. As might be expected in an immature individual, there is little evidence of secondary bone apposition.

The third ossicone (SAM–PQ–L30960) is somewhat larger but is incomplete distally. The rugose nature of the bone within the basal cavity suggests that this specimen, too, was derived from an immature individual.

Dentition

A few nearly complete lower tooth rows are known but the majority of Langebaanweg giraffine teeth were isolated specimens. The teeth are, in general, a little larger than those of the extant *Giraffa camelopardalis* and than Eurasian fossil giraffine species (*G. priscilla, G. attica, G. punjabensis, G. sivalensis*). Though larger than the teeth from the type specimen of *G. jumae* from Rawe (Leakey 1965) they are of similar size to teeth of Late Pliocene and early Pleistocene specimens of *G. jumae* from other east African localities (Harris 1976, and in preparation).

Postcranial remains

The Langebaanweg giraffine postcranial elements have typical giraffine morphology. They are of similar size and proportions to those of extant male giraffes, larger than specimens of *G. jumae* from the Omo Basin (Coppens *et al.*, in preparation) but of similar size to the largest *G. jumae* specimens from the Ethiopian locality of Hadar (Taieb *et al.* 1974; Harris, in preparation). Differences in postcranial anatomy between the Langebaanweg giraffine and *Sivatherium hendeyi* have been discussed previously in this paper.

Remarks

In the absence of mature ossicones, whose orientation on the cranium can be determined, it is difficult to make a positive identification of the Langebaanweg giraffine. The known specimens are too large for *Giraffa pygmaeus* and the presence of a distinct terminal knob suggests that they do not belong to *G. gracilis.* They are slightly smaller than, but otherwise quite similar to, immature ossicones of *Giraffa camelopardalis* but could equally well belong to *G. jumae* (immature specimens of which are yet unknown) or even a new species. None of the three east African fossil giraffine species is clearly ancestral to *Giraffa camelopardalis* and the possibility that the extant giraffe was of South African origin, and perhaps descended from the Langebaanweg form, cannot be entirely ruled out. The acquisition of mature giraffine ossicones from Langebaanweg may in future solve the problem. Meanwhile, because the teeth are rather larger than those of extant giraffes and, on balance, the postcranial elements are rather more robust than the latter, the Langebaanweg giraffine is provisionally assigned to *Giraffa* cf. *G. jumae*.

TABLE 6

Measurements of *Giraffa* cf. *G. jumae* ossicones

	L20940 (l)	L20940 (r)	L30690
Length	177	177	
Basal diameter ap	86	92	112
Basal diameter tr	59	59	

TABLE 7

Measurements of *Giraffa* cf. *G. jumae* deciduous teeth

	L6606	L13510	L13043 (l)	L13043 (r)	L10938	L10939	L10800
DP^2 ap			23,3	23,3	24,3		
tr			19,4	19,7	17,4		
DP^3 ap	26,1		27,1	26,8		27,7	28,8
tr	21,8	20,3	22,6	23,7		24,4	26,5
DP^4 ap			27,5	28,2			
tr			27,4	28,3			
	L30057	L2543	L6022	L11617	L2541		
DP_2 ap	19,6						
tr	10,9						
DP_3 ap	25,8						
tr	14,4						
DP_4 ap	36,2	38,2	32′		33,9*		
tr	19,1	18,6	17′	16,5′	18,6′		

TABLE 8

Measurements of *Giraffa* cf. *G. jumae* upper teeth

	L30126	L22021	L31138	L10343 (l)	L10343 (r)
P^2 ap		22,3			
tr		26,5			
P^3 ap	25,0				
tr	27,4				
P^4 ap	25,6				
tr	28,2				
M^1 ap				31,3	29,2
tr				33,1	33,7
M^2 ap			33,0	33,4	31,6
tr			37,1*	34,8	36,1
M^3 ap			35,2		
tr			36,8		

TABLE 9

Measurements of *Giraffa* cf. *G. jumae* lower teeth

	L22021	L5767	L31138	L20987	L4773
P_2 ap			23,0		
tr			14,4		
P_3 ap			27,0	23,6	
tr			20,1	19,7	
P_4 ap			28,5	24,4	26,1*
tr			22,7	22,1	20,6
M^1 ap	27,5		33,1	27,5	
tr	22,2	23,5	23,7	24,4	
M_2 ap		31,3	32,9	30,0	
tr		25,3	25,3	24,6	
M_3 ap			46,9		
tr			25,0		

TABLE 10

Measurements of postcranial elements of *Giraffa* cf. *G. jumae*

HUMERUS	L9933	L3095	L12372	L20951	L14148	L6950	L6355	L6884	L6949
Width lat epicondyle	117	126		127	124	123			138
Width distal epiphysis	115	121		138	119	128			134
Depth distal epiphysis	110	113	85+	99	96	90	81+	77+	103

ULNA	L6037	L13500
Depth olecranon process at epiphysis junction	93	94
Width humerus facet tr	65	59
Depth humerus facet ap	65	60

RADIUS	L4962	L7922	L7994	L5233	L13500
Proximal epiphysis tr	134		118		129
ap	75		68		69
Distal epiphysis ap		108		119	
tr		79		89	

METACARPAL	L22282	L20859	L11509	L13687	L6035	L5488	L12734A	L7268	L5303	L7267	L9282	L7264
Proximal epiphysis ap	66		70	66	70	64	68	63	64			
tr	99		98+	103	98	96+	105	95	97			
Distal epiphysis ap		65								58+	66	60
tr		96								99		88

TIBIA	L1797	L13528	L14308	L11527	L6030	L20863	L20866	L14352
Length	655	590						
Prox ap							121	
tr		156						
Dist ap	89	76	86	92	80	64		82
tr	114	113	114	120+	111	94		114

FIBULA	L13001	L12231
Max length ap	71	70
Max breadth tr	36	34
Max height dv	53	46

Table 10 (*continued*)

CALCANEUM	L4875	L14193	L11568	L4879	L7369	L20268	L2230	L21818	L5897	L4228	L20629	
Max length	213	238	233	209	196	224	228	205			192	
Max articular width	99	106	85	80	86	96	85	87	77	66		
Max articular depth	105	108	93	93	92	114	107	97	99	84	91	
Width tuber cacis	67	77	68	52	50	67	64	55			53	
Depth tuber calcis	63	81	80	63	58	75	71	57				
ASTRAGALUS	L4919	L20852	L7386	L1241	L2082	L9826	L20950	L1241	L12184	L21913	L24920	
Lat length	107	123	107	111	119	115	116	107	111	118	126	
Med length	97	104	97	98	110	104	102	94	100	108	106	
Tibial trochlea tr	72	82	70	72	72		78	76	75	81	89	
Navcbd trochlea tr	64	74	69	67	70	69	74	68	75	74	80	
Max depth	58	67	64	58	67		64	63	61	68	71	
	L14190	L5400	L11754	L9218	L7388	L12384	L4224	L7383	L22180			
Lat length	122	115	125	105	115	116	118	109	128			
Med length	107	97	107	92	101	99	104	98	110			
Tibial tr	84	85	85	71	73	74	79	69	79			
Navcbd tr	79	78	75	65	73	70	74	64	79			
Max depth	71	72	74	59	61	63	67	60	76			
NAVICULOCUBOID	L5158	L5159	L1264	L6100	L11571	L3897	L7360	L7353	L7356	L7357	L7365	L7354
Med length ap	103	101	89	97	98			108		106	93	
Max width tr	97	96	91	87	95	86	89	103	93	91	87	87
Lat height dv	45	51	50	47	46	48	48	50	47	54	49	47
METATARSAL	L6227	L5304	L7282	L22158	L14188	L6069						
Prox ap	87		92		98							
tr	85		84		94							
Dist ap		60		59		64						
tr		86		88		87						

DISCUSSION

The giraffoids from Langebaanweg are almost certainly the earliest representatives of their respective genera yet reported from Africa although confirmation of their age must await detailed investigation of other elements of the fauna. If an early Pliocene age is substantiated the two Langebaanweg giraffoids are of similar if not earlier age than their nearest Asian relatives and the question of Asian versus African origin of the giraffines and later sivatheriids will need to be reinvestigated.

Hamilton (1973) assigned *Prolibytherium* to the Sivatheriidae and suggested that sivatheriids and giraffids were independently derived from Oligocene Dremotheriidae. *Prolibytherium* shares many morphological features with dremotheriids and primitive cervids and may, perhaps, be better assigned to one of these families. The evidence for sivatheriid affinity is not conclusive and, as Hamilton himself points out (1973, fig. 13), if placed in the Sivatheriidae *Prolibytherium* can be only distantly related to other known members of the family.

As is evident from *Sivatherium hendeyi*, a foreshortened anterior limb is not a primitive feature of *Sivatherium* but a character acquired during the evolution of this genus. Moreover, the posterior ossicones of *S. hendeyi* are relatively short, narrow and unornamented, suggesting that the palmate posterior ossicones of *S. giganteum* and the more complex examples of *S. maurusium* are advanced features. The disposition of the ossicones of *S. hendeyi* is not dissimilar to that of *Giraffokeryx* (Colbert 1933). It is not implausible that *Sivatherium* and related genera were relatively late (upper Miocene?) offshoots from paleotragine stock. If so, relegation of the family Sivatheriidae to a subfamily of the Giraffidae might appear warranted.

Abundant giraffine material is known from Hadar in Ethiopia (Harris, in preparation) and Laetolil in Tanzania (Harris, in preparation). The earlier horizons from Hadar are dated in excess of 3 m.y. (D. C. Johanson, pers. comm.) and the Laetolil faunas are believed to be between 3,25 and 3,75 m.y. (M. D. Leakey, pers. comm.). Occurring at both localities are representatives of the three species known from east African Pleistocene localities. Giraffines have not yet been reported from Lothagam and Kanapoi but a few undescribed and incomplete specimens are known from Lukeino which have been dated at between 5,4 and 6,7 m.y. (Pickford 1975). The subfamily Paleotraginae is currently being revised (W. R. Hamilton, pers. comm.) and perhaps in the near future further east African material will be available to help place the Langebaanweg giraffines in their proper context.

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ABBREVIATIONS

ap	anteroposterior	Lat	lateral
dv	dorsoventral	prox	proximal
tr	transverse	dist	distal
	estimated measurement	med	medial
*	approximate measurement	navcbd	naviculocuboid
Max	maximum	tr	trochlea (astragalus measurements only)